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Priming effect and C storage in semi-arid no-till spring crop rotations

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Abstract Adoption of less invasive management practices, such as no-till (NT) and continuous cropping, could reduce CO_2 emissions from agricultural soils by retaining soil organic matter (SOM). We hypothesized that C storage increases as cropping intensity increases and tillage decreases. We also hypothesized that pulsed addition of C increases the mineralization of native SOM. We evaluated C storage at the 0- to 5-cm depth in soils from four crop rotations: winter wheat-fallow, spring wheat-chemical fallow, continuous hard red spring wheat, and spring wheat-spring barley on a Ritzville silt loam (Calcidic Haploxeroll). In two incubation studies using ^{14}C-labeled wheat straw, we traced the decomposition of added residue as influenced by (1) cropping frequency, (2) tillage, and (3) pulsed additions of C. Differences in ^{14}C mineralization did not exist among the four rotations at any time throughout the incubations. However, differences in total CO_2 production between the continuous wheat rotations and the fallow rotations point to a priming of native SOM, the degree of which appears to be related to the relative contributions of fungi and bacteria to the decomposition of added residue. Addition of non-labeled wheat straw to select samples in the second incubation resulted in a flush of ^{14}C-CO_2 not seen in the controls. This priming effect suggests C inputs have a greater effect on mineralization of residual C compared to disturbance and endogenous metabolism appears to be the source of primed C, with priming becoming more pronounced as the fungal:bacterial ratio in the soil increases.

Keywords Organic matter · C decomposition · C storage · Crop rotation · C sequestration

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Introduction

In response to rising levels of atmospheric greenhouse gases, adoption of no-till (NT) and continuous cropping could reduce CO_2 emissions from agricultural soils by increasing soil C through the retention of soil organic matter (SOM). Adoption of such practices is appealing due to the promising benefit of improved soil quality through reduced erosion, increased structural stability, and decreased oxidation of SOM. In addition, the potential for crop producers to gain carbon credits through adopting management practices that sequester C in the form of SOM makes incorporating practices such as NT more appealing. However verifying the actual storage of C and its consequent measurement is proving to be a challenge (Rosenberg and Izaurralde 2001). While the effect of tillage and crop rotations on SOM levels in soil is well documented (Campbell et al. 1999; Janzen 1987; Lal 1997; Smith and Elliott 1990; Staben et al. 1997), few data are available on how the frequency of residue input affects C-storage.

Conversion of native grassland soils to cropland has led to significant losses of soil organic C ranging from 20% to more than 50% (Haas et al. 1957; Tiessen et al. 1982). Many studies have reported significantly higher levels of SOM in soils under reduced tillage. For example adoption of NT in areas of the Canadian Prairie resulted in a soil C increase of 4 Mg C ha^{-1} after a period of 11 years (Campbell et al. 1996). Similarly Arshad et al. (1990) found NT soils contained 26% higher levels of C compared to similar soils under conventional till. A wheat-fallow rotation comparison of tillage systems showed that as tillage decreased, loss of C also decreased (Halvorson et al. 1997; Lyon et al. 1997; Peterson et al. 1998;). The reduced tillage-increased soil C effect is due to decreasing the mixing and aeration of residues and the promotion and stabilization of aggregates, especially in the surface soil layers.

Crop rotation also has a direct impact on organic matter levels in surface soil (Bremer et al. 1995; Janzen et al. 1992). In semi-arid areas, winter wheat-summer fallow

is the traditional crop rotation. However problems associated with fallow, such as increased erosion and loss of organic C and N, are prevalent (Peterson et al. 1998). Several studies investigating the effect of fallow-containing rotations on SOM have found levels of labile SOM to decrease as frequency of fallow increases (Biederbeck et al. 1994; Campbell et al. 1992; Collins et al. 1992). Additionally, combining NT with continuous cropping will have the greatest increase in surface soil organic C (Potter et al. 1997). This effect is due to increased residue additions along with reduced oxidation; however, the influence of reduced tillage and crop rotation does not appear to be additive (Pankhurst et al. 2002).

The objectives of this research were to (1) assess residue C dynamics in NT soils under spring cropping systems and (2) determine the effect residue inputs have on mineralization of labile SOM. We hypothesize that C storage increases as cropping frequency increases and tillage decreases. In addition, we hypothesize that addition of C increases the mineralization of native SOM. Results of this study will help us better understand the characteristics of residue decomposition under NT and continuous cropping. This information can then be used in developing strategies to improve soil quality, reduce CO_2 emissions from agricultural soil, and verify increases in soil C sequestration.

Materials and methods

Study area and soil sampling

The study area was located in the semi-arid region of Washington State, USA. The mean annual temperature is 12°C and annual precipitation is 23–30 cm. A NT spring cropping systems project was established on a dry-land wheat farm near Ralston, Wash., during the summer of 1995 to investigate alternatives to the conventional winter wheat-fallow rotation. This ground was previously managed under a winter wheat fallow rotation using tillage and herbicides to control weeds during the fallow period.

The soil is classified as a Ritzville silt loam (Calcidic Haploxeroll). Four crop rotations of winter wheat fallow (WW-F), NT spring wheat-chemical fallow (SW-CF), NT continuous hard red spring wheat (HRSW), and NT spring wheat-spring barley (SW-SB) were established in either winter wheat stubble or fallow in a randomized block design (152×9 m). The WW-F rotation, managed under conventional tillage, was the control to which the three NT rotations were compared. The WW-F and SW-CF rotations were cropped every other year and the continuous rotations were cropped every year. Weeds were controlled by tillage and herbicides in WW-F and herbicide application in the three NT rotations, with SW-CF receiving 50% more herbicide inputs compared to the continuous NT rotations as a result of the fallow period.

The rotation phase at the time of sampling, denoted by capital letters, was ww-F, sw-CF, HRSW, sw-SB. Samples were taken by hand spade at two depths (0–5 cm and 5–10 cm) from six to eight random locations within each rotation plot then composited. Soils were sieved to 2 mm and stored at 4°C until further analyses were carried out.

Soil analyses

Selected soil characteristics for the surface 0–5 cm are summarized in Table 1. Total C and N were determined by dry combustion using a CNS-2000 Leco analyzer. Dispersing 10 g soil in 30 ml 0.5 M sodium hexametaphosphate and passing the mixture through a 53-μm sieve separated the particulate organic matter (POM) fraction (>53 μm) from the mineral fraction (<53 μm) (Cambardella and Elliott 1992). Organic C and total N in the POM and mineral fractions were determined by dry combustion using a CNS-2000 Leco analyzer. Soil pH was taken in a 1:1 soil:water extract using a glass electrode. Moist soil (6 g) was extracted with 2 M KCl (6 g:25 ml) and analyzed for inorganic N using a 300 series Alpkem continuous flow analyzer. Microbial biomass was determined using fumigation extraction (Joergensen 1995; Vance et al. 1987). Fungal to bacterial ratios (F:B) in the soil were determined with the selective inhibition method using Captan (fungicide) and Bronopol (bactericide) as inhibitors (Bailey et al. 2002).

Experiment 1: labeled wheat straw mineralization

The laboratory incubation was conducted in a closed-jar system at 25°C for 31 days. Labeled plant material was obtained by growing spring wheat to maturity in an atmosphere of $^{14}CO_2$. The dried wheat straw was ground to 500 μm (32 mesh) and tested to insure that no material passed a 53-μm sieve. The labeled wheat straw N content was 0.37% N. Triplicate samples of 30 g soil (dry weight) from the surface 0–5 cm of each rotation were amended with 1.54 mg ^{14}C-labeled wheat straw (3,200 dpm mg^{-1} C) g^{-1} soil. Three levels of N-urea solution were added to triplicate samples at the following rates: zero, 25, and 50 μg N g^{-1} soil. The final soil water potential at the start of the incubation was 10 kPa (20% w/w). Labeled straw decomposition was measured by trapping evolved CO_2 in vials containing 1 ml 1.0 M NaOH. An aliquot of 0.25 ml was removed from the vial for liquid scintillation counting to determine ^{14}C activity. The remaining 0.75 ml was used to determine total CO_2 by acid titration. Triplicate subsamples of unamended soil were incubated simultaneously under similar conditions and analyzed as described above for total CO_2.

A similar set of triplicate samples were amended as above for the purpose of destructive sampling on days 3, 6, 10, 17, 24, and 31. Microbial biomass C (MBC) was determined using fumigation-extraction (Joergensen 1995; Vance et al. 1987), and unfumigated subsamples were used as controls. Biomass ^{14}C was calculated

Table 1 Selected soil physical, chemical, and microbiological characteristics (0–5 cm). *Similar lower case letters* denote significant differences between rotations (P =0.01). *ww-F* Winter wheat fallow, *sw-CF* no-till (NT) spring wheat-chemical fallow, *HRSW* NT continuous hard red spring wheat, *sw-SB* NT spring wheat-spring barley, *POM* particulate organic matter, *F:B* fungal:bacterial ratio

Rotation	Total C kg C/ha	Total N kg C/ha	POM C g/kg soil	POM N g/kg soil	pH	F:B ratio	Microbial biomass μg C/g soil
ww-F[a]	5,407a	483a	3.81a	0.22a	6.5a	0.77a	420a
sw-CF	5,735a	476a	3.92a	0.24a	6.4a	0.36b	540a
HRSW	6 053b	427a	5.21b	0.30a	6.3a	0.56c	632b
sw-SB	5 962b	508a	4.77b	0.28a	6.6a	1.09d	883b

[a] Capital letters denotes rotation phase at time of sampling

from the increase in extractable ^{14}C after fumigation, multiplied by 3.25 (Ladd and Amato 1988). The POM was isolated by dispersing approximately 5 g soil (DW) in 5 g l^{-1} sodium hexametaphosphate and passing the mixture through a 53-μm sieve (Cambardella and Elliott 1992). The organic C and ^{14}C in POM was determined using wet oxidation (Snyder and Trofymow 1984).

Experiment 2: pulsed C additions

Soils from the WW-F and NT HRSW rotations were incubated in closed jars for 40 days in a similar fashion as in Experiment 1. Eight replicate subsamples of 30 g soil (dry weight) were amended with 1.54 mg ^{14}C-labeled wheat straw (3,200 dpm mg^{-1} C) g^{-1} soil. Soil water potential was adjusted to 10 kPa (20% w/w) at the start of the incubation. The CO_2 evolved was trapped in vials containing 1 ml 1.0 M NaOH and total CO_2 determined by acid titration. Liquid scintillation was used in determining ^{14}C activity.

On days 17 and 27 all samples were hand-stirred and non-labeled straw (1.54 mg C g^{-1} soil) added to six of the eight samples (D+^{12}C). The remaining two acted as controls and were hand-stirred only (DO). Evolved CO_2 and ^{14}C activity were measured as stated previously.

Statistical analysis

The statistical design of the field experiment was a randomized block design with four treatments and four blocks. Since the treatments were stratified within blocks interaction terms are inappropriate, thus we used a GLM for statistical analysis of blocks and treatments (SPSS 1998). No significant block effects were observed, thus the reported statistics (P values) are treatment (rotation) only comparisons. Significant differences (P values) between treatments (rotation) for any variable were determined using Bonferroni pairwise comparisons. The significant differences for CO_2 evolution were made for specific time periods, not repeated measures, using the same GLM as for static parameters and Bonferroni pairwise comparisons for P values.

Results

The effects of NT, spring cropping and N additions on the mineralization of ^{14}C-labeled wheat straw were compared in this study. Samples from the conventionally tilled WW-F rotation acted as controls to which samples from three NT rotations (SW-CF, HRSW, and SW-SB) were compared. The addition of 25 and 50 μg N g^{-1} soil as urea solution did not significantly affect the mineralization of the added wheat straw in any of the rotations (data not shown). During the 2000 growing season, the region in which the study site is located experienced drought conditions resulting in low yields. Consequently a large residual inorganic N pool (in excess of 40 μg N g^{-1} soil) was present at the time of sampling, providing explanation for why supplemental N did not increase C mineralization as expected. Since there were no significant differences among the zero, low, and high N treatments, data presented from this point forward will be from the low N (25 μg N g^{-1} soil) treatment.

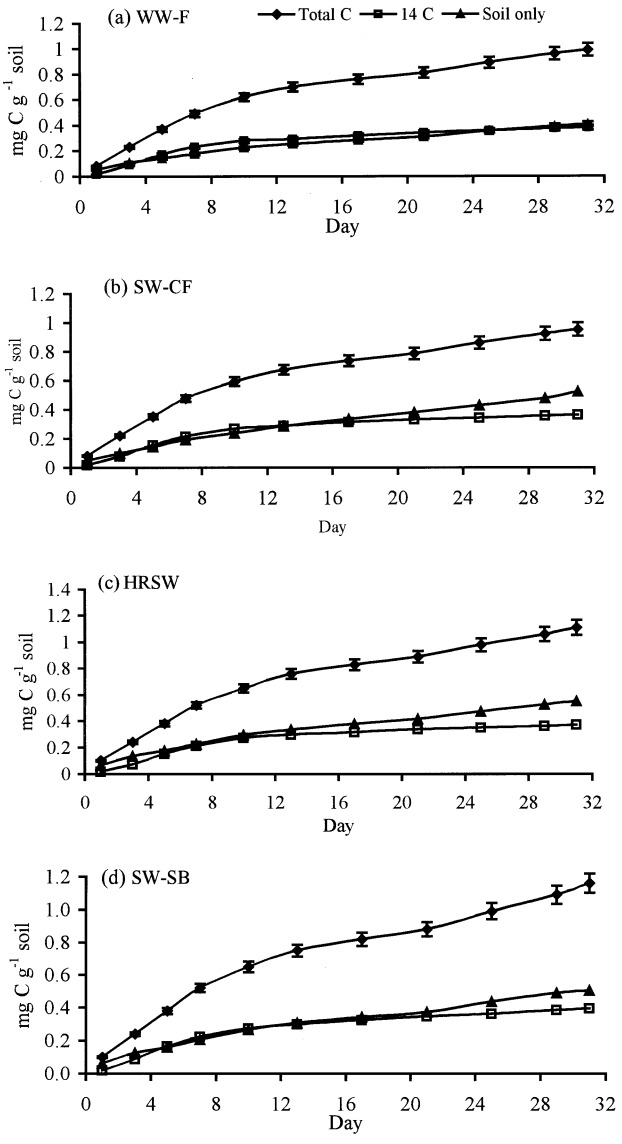

Fig. 1 Effect of ^{14}C additions on the mineralization of native soil organic matter in WW-F (**a**), SW-CF (**b**), HRSW (**c**) and SW-SB (**d**). Standard errors are indicated or are less than symbol size

Labeled wheat straw mineralization

Incorporation of the labeled wheat straw resulted in an initial rapid rate of CO_2 production lasting approximately 7 days after which CO_2 production slowed (Fig. 1a–d). The three NT rotations were similar to WW-F until day 7 when the CO_2 production from the NT continuous wheat rotations became significantly higher (P <.001) than both WW-F and SW-CF. By the end of the incubation, total cumulative CO_2 production from the SW-SB rotation was significantly higher than HRSW (P =031). Cumulative total CO_2 production in the WW-F and SW-CF rotations did not differ significantly, however CO_2 production in the WW-F rotation was slightly higher than SW-CF by the end of the incubation.

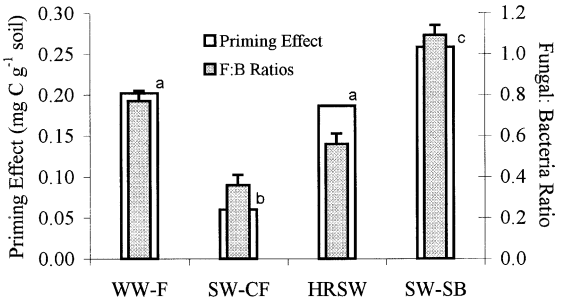

Fig. 2 Quantification of priming effect and fungal:bacterial (*F:B*) ratios among rotations. *Bars denoted by a different letter* differ significantly in priming at $P \leq 0.05$. *Error bars* denote standard error for F:B ratios

Mineralization of the added wheat straw began immediately and was the same for all rotations (Fig. 1a–d). By the end of the incubation, 28% of the added ^{14}C had evolved as CO_2. A turnover of ^{14}C, indicated by a rise and fall in CO_2 specific activity, occurred approximately every 12 days with subsequent peaks in specific activity being smaller than the previous cycle (data not shown).

A priming effect, suggested by the similar mineralization of the added ^{14}C-wheat straw among treatments but differences in total CO_2 production, is shown in Fig. 1a–d and quantified in Fig. 2. Comparison of the $^{12}CO_2$ evolved from the amended samples (total CO_2-$^{14}CO_2$) to the CO_2 evolved from the soil only samples, yielded priming effects of 0.20, 0.06, 0.19, and 0.26 mg C g^{-1} soil for WW-F, SW-CF, HRSW, and SW-SB, respectively. Priming in the SW-CF and SW-SB rotations was significantly different from WW-F (P =0.002 and P =0.001, respectively). No significant difference was detected between the HRSW and WW-F rotations (Fig. 2). There was a significant correlation (P <0.01) between priming and the F:B ratios of all treatments (Fig. 2).

Partitioning of substrate derived C

Periodic destructive sampling during the course of the experiment allowed us to trace the flow of ^{14}C in the soil. Size fractionation of SOM showed the majority of the added ^{14}C remained in the POM fraction (Fig. 3a); however, approximately 10% of the added ^{14}C had moved into the mineral (<0.53 μm) organic matter fraction within the first 3–6 days of the experiment. There was no further movement of ^{14}C between these two fractions after this time. Continued loss of POM-^{14}C during the incubation is due to mineralization (Fig. 3a).

Initial incorporation of ^{14}C into microbial biomass occurred at rates ranging from 0.42% to 0.71% of added ^{14}C per day (Fig. 3b). The specific activity of the WW-F biomass peaked on day 17 then slowly declined with 3.4% remaining in the biomass at the end of the incubation. Specific activity of biomass in the NT rotations peaked on day 3 then steadily decreased. By the end of the experiment 4.6% remained in the HRSW

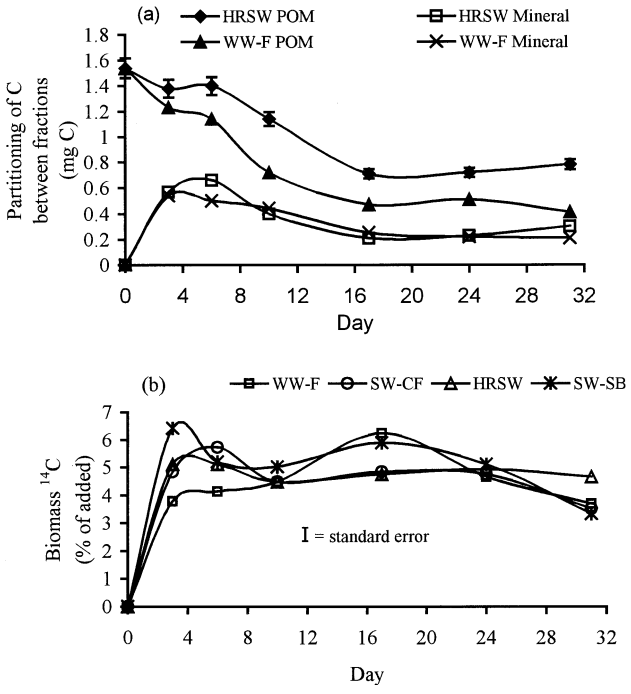

Fig. 3 Destructive sampling results: **a** soil organic matter (*SOM*) fractionation and **b** microbial biomass C. Standard errors are indicated or are less than symbol size

biomass and approximately 3% remained in SW-CF and SW-SB.

Effect of disturbance and addition of ^{12}C on residual ^{14}C mineralization

The combined effects of disturbance and addition of non-labeled wheat straw (D+^{12}C) on the mineralization of residual ^{14}C organic matter were compared to the singular effect of disturbance only (DO). The effects were similar for both rotations (WW-F and HRSW) used in this experiment, so for simplicity only the results from the HRSW rotation will be discussed in detail.

Following incorporation of the labeled wheat straw, cumulative total CO_2 production was similar to that in the first experiment. Figure 4a shows an initial rapid rate of mineralization lasting approximately 9 days after which CO_2 production slows. On day 17 disturbance of the DO samples resulted in a slight, though not significant, increase in CO_2 evolution. Another disturbance of the DO samples on day 27 had no further effect on CO_2 evolution. However, when non-labeled wheat straw was incorporated into the D+^{12}C samples at the time of disturbance, there was a significant increase in total CO_2 evolution (Fig. 4a). On day 27 a subsequent addition of non-labeled wheat straw to the D+^{12}C samples produced a similar flush as the first addition. As expected, by the end of the experiment cumulative total CO_2 for the D+^{12}C samples was significantly higher than total cumulative CO_2 for the DO samples (P <.001).

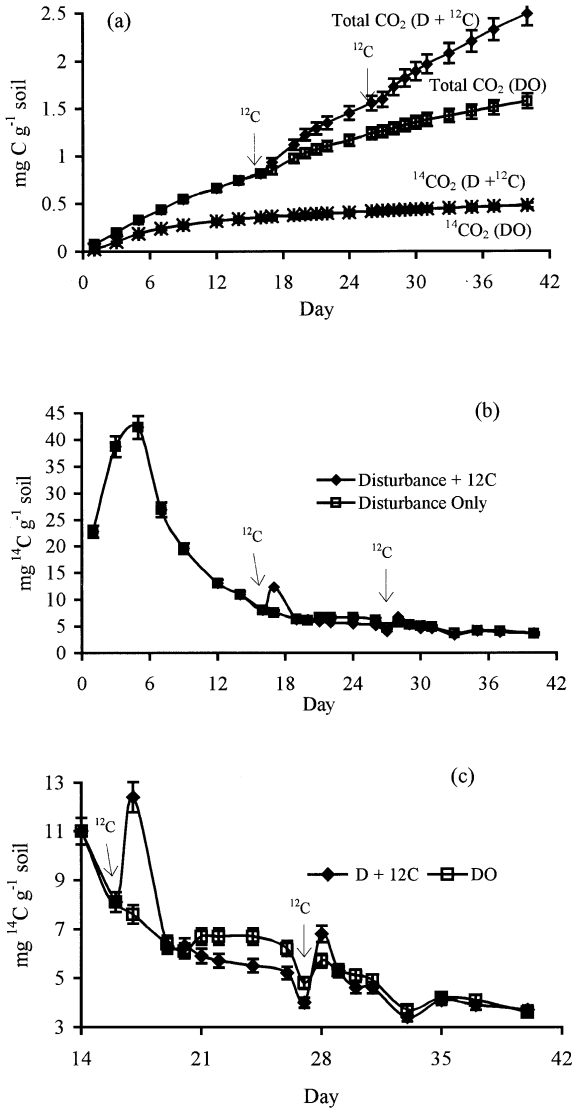

Fig. 4 Effect of adding ^{12}C wheat straw on decomposition of ^{14}C-labeled soil organic matter on **a** cumulative CO_2 and $^{14}CO_2$ production, **b** rate of $^{14}CO_2$ production days 1–40 and **c** days 14–40. Standard errors are indicated or are less than symbol size

Mineralization of the ^{14}C-labeled wheat straw added at the beginning of the experiment began immediately with the maximum rate of mineralization occurring within 5 days (Fig. 4b). By day 17, 23% of the added ^{14}C had evolved as $^{14}CO_2$. Disturbance of the DO samples on day 17 did not cause a flush in $^{14}CO_2$ evolution; however 3 days after disturbance occurred, $^{14}CO_2$ evolution began to increase slightly rising above that of the D+^{12}C samples (Fig. 4c) and remained elevated for a period of 7 days. The second disturbance in the DO samples on day 27 had no further effect on the evolution of $^{14}CO_2$. Addition of non-labeled wheat straw to the D+^{12}C samples on day 17 resulted in an immediate peak in $^{14}CO_2$ evolution lasting approximately 1 day after which there was a steady decrease. A subsequent addition of non-labeled wheat straw on day 27 again stimulated $^{14}CO_2$ evolution in the D+^{12}C samples but to a lesser extent than the first. For the remainder of the experiment, there was no significant difference in $^{14}CO_2$ evolution for both the D+^{12}C and DO samples.

Discussion

The storage of C in soil is a function of residue inputs, decomposition rates and soil texture. In agricultural soils there is the added complexity of tillage and crop rotation. By decreasing tillage and increasing rotations it is hoped that soil C can be increased and the multitude of benefits of SOM can be obtained (Smith 2002). However, there are competing processes in soil systems which may interact and decrease the desired or expected impact. We assume that the cycling of C upon addition of crop residues is a function of not only the size of the microbial biomass but of the composition of the microflora. Furthermore, we assume that the microbial metabolic efficiency plays a role in the long term C storage of crop residues.

Added wheat straw decomposition measured as CO_2 followed a familiar cumulative hyperbolic curve (Fig. 1a–d) (Knapp et al. 1983a; Ladd et al. 1995, 1996; Saggar et al. 1999). Initially $^{14}CO_2$ made up 60% of the total CO_2 during the first phase of decomposition (data not shown) and still accounted for 20% of the total CO_2 produced on day 31. This trend was similar for all rotations; however the differences among the rotations in total CO_2 production at the end of the experiment suggests inputs of straw residue may effect C storage in soils by stimulating turnover of native ^{12}C. Possible sources for the ^{12}C priming include decomposition of native SOM and/or endogenous metabolism in the soil microflora defined as turnover of ^{12}C in the microbial biomass due to the assimilation of easily decomposed ^{14}C compounds (Jenkinson et al. 1985; Smith et al. 1985).

Since priming continued throughout the incubation (Fig. 1) more than one factor may be contributing to the priming effect. Detailed studies to investigate the cause and/or factors contributing to the dynamics of priming are lacking (Kuzyakov et al. 2000). In this study, as well as others of a similar nature, it is difficult to pinpoint whether the source of primed ^{12}C is from residual SOM or endogenous microbial metabolism. Priming effects of added substrates have been reported previously (Dalenberg and Jager 1989; Jenkinson et al. 1985; Magid et al. 1999) with turnover of microbial biomass C generally accepted as the source of primed C. The assumption of biomass-derived primed C is supported by the results of our second experiment in which a flush of $^{14}CO_2$ was detected immediately after addition of ^{12}C. The priming effect in the D+^{12}C samples of the second experiment (Fig. 4b, c) can be attributed to turnover within the soil microflora rather than further decomposition of residual SOM as also found by Dalenberg and Jager (1981, 1989). The absence of a ^{14}C flush in the DO samples of the second experiment further supports the assumption that

Table 2 Effect of rotation on straw C inputs

Rotation	Straw C (kg ha^{-1})					5-year average[b]
	1996	1997	1998	1999	2000	
WW-F	2,648	–[a]	2,601	–	2,512	1,552a
SW-CF	1,729	–	2,216	–	1,724	1,134a
HRSW	1,470	1,860	1,420	1,101	1,155	1,402a
SW-SB	1,449	2,095	1,508	1,163	1,329	1,509a

[a] *Dash* indicates fallow period and no straw C input for the growing season
[b] *Lower case letters* indicate significant difference among rotations (P =0.001)

priming occurred due to a reduction in the microbial-specific activity caused by dilution of biomass ^{14}C by ^{12}C rather than decomposition of SOM. It appears that metabolism of easily decomposable ^{12}C compounds from the added straw resulted in a flush of endogenous ^{14}C reserves from the microbial biomass.

In this study the size of the microbial biomass was significantly correlated to the soil total C (r =0.76), soil POM C (r =0.66) and to the priming effect in the no-till rotations (r =0.91). It can be theorized that the noted differences in microbial biomass (Table 1) are due to differences in the frequency of residue inputs (Table 2) rather than the total residue input amounts. In these rotations there was no significant difference in the amount of straw C input among the NT spring wheat rotations and the WW-F rotation (Table 2), however, there are significant differences in the frequency of the straw inputs. The buildup of labile C and microbial biomass in the continuous cropped NT soils is due to frequency (i.e. yearly) of residue inputs and the lack of soil disturbance and thus reduced oxidation of organic matter (Peterson et al. 1998; Mrabet et al. 2001; Pankhurst et al. 2002). When fallow is incorporated into a rotation, inputs of crop residue occur only when a crop is planted and, under these conditions, the depletion of the easily decomposable C pool after one growing season forces microflora to metabolize secondary pools of C (i.e. POM and intermediate C) during the fallow period. For this reason, rotations with fallow periods generally contain lower levels of labile C (Campbell et al. 1999) and support lower levels of microbial biomass (Smith and Elliott 1990).

While crop rotation and tillage determines the amount of labile C in the soil and the size of the microbial biomass, the F:B ratio of the microbial biomass appears to be a driving factor in priming of ^{12}C in these soils. Indeed, the F:B ratio was significantly correlated to the priming effect in all treatments (r =0.92) and as the F:B ratio increased, priming effect also increased (Fig. 2). In the NT soils, F:B increased from 0.36 to 1.09 for SW-CF and SW-SB, respectively, with HRSW being intermediate at 0.56. The F:B ratio for the WW-F rotation was 0.77 (Table 1). In all soils the cumulative priming increased approximately linearly to day 12 of the incubation then continued to accumulate at a sharply reduced rate (data not shown). The first phase of the priming is attributed to bacterial growth and endogenous metabolism and the slower second phase to fungal contributions. In the SW-CF rotation, bacteria accounted for approximately 73.5% of the microbial biomass and priming was the lowest of all rotations. Bacteria quickly metabolize the soluble C compounds associated with recent residue inputs; therefore, it can be assumed that bacterial-driven priming would occur soon after residue addition (Lundquist et al. 1999) and be short lived due to the relatively small pool of soluble C in wheat straw (Knapp et al. 1983b). As the F:B ratio approached a value of 1.0, indicating that fungi and bacteria equally contribute to the decomposition of SOM, priming increased (Fig. 2). As decomposition progresses fungi are more efficient at metabolizing residual C complexes (Bottomley 1999; Lundquist et al. 1999) extending the time frame of when priming would occur in the system. Increases in priming when fungi are more numerous can be attributed to cooperative decomposition with bacteria (Bottomley 1999). In cooperative decomposition fungi break down more resistant C complexes in residues, and simpler C compounds become available for bacterial consumption. Thus in soils with larger F:B ratios, the extent and duration of priming can be expected to be more pronounced as seen in the NT continuous wheat and WW-F rotations.

Similar priming was observed in the WW-F (202 μg C g^{-1} soil) and HRSW (187 μg Cg^{-1} soil) rotations, despite differences in microbial biomass. In addition, the F:B ratios were different with the greater F:B ratio in the WW-F system, which may provide an explanation for the observed similarities in priming. The differences in priming early in the incubation support our hypothesis that the composition of the soil microflora regulates priming in the soil. The initial rapid release of ^{12}C from the HRSW (Fig. 1c) and the WW-F soil (Fig. 1a) during the first 7 days is similar and consistent with bacterial-driven priming and accounted for less than 50% of the total ^{12}C primed from either rotation. At this time the release from endogenous metabolism was complete, with a sharp reduction in CO_2-specific activity in both rotations (data not shown). From day 7 to 13 it would appear that cooperative decomposition is occurring by the higher rates of priming in the WW-F soil with a higher F:B ratio. During this period there was a 60% greater priming effect in the WW-F soil compared to the HRSW soil showing that the extended duration of this initial priming rate can be explained by the cooperative decomposition between fungi and bacteria mentioned previously. This indicates that the F:B ratio affects priming because of its connection to cooperative decomposition

more so than the absolute amount of microbial biomass. From this we can conclude that the extended duration of the initial rapid rate of priming results in greater amounts of residual C being primed, with this effect becoming more pronounced as the F:B ratio increases.

The C storage of added residue can be calculated from the $^{14}CO_2$ data and the original amount added. The remaining amounts of added residue in the soil were similar with SW-SB being the lowest at 1.09 mg C g^{-1} soil to SW-CF retaining 1.13 mg C g^{-1} soil, WW-F and HRSW being intermediate sequestering 1.11 and 1.12 mg C g^{-1} soil, respectively. In considering total C storage from residues the priming effect has to be considered since it is labile C lost from the system. The primed C due to residue addition as a percentage of the added C that remained at the end of the incubation ranged from 17% in the HRSW rotation to 24% in the SB-SW rotation. The SW-CF had a low priming effect due to a combination of small labile C pools and a low fungal population possibly due to increased herbicide inputs. The WW-F rotation had a primed C/stored C ratio of 18%. Again, however, the size of the microbial biomass needs to be considered when determining the C storage of a soil. The microbial biomass of the WW-F rotation is 50% less than the microbial biomass of the SW-SB rotation, meaning that per unit microbial biomass more CO_2 was evolved from the WW-F rotation. This suggests the WW-F is an inefficient system where residue inputs are probably exhausted with little C storage. Further support for differences in C storage can be seen from the calculation of the metabolic quotient or basal respiration to biomass ratio (qCO_2) from the untreated control soils at the end of the 31-day incubation (Smith 2002). The metabolic efficiencies averaged 8.4×10^{-4} μg CO_2-C μg^{-1} biomass C h^{-1} for WW-F and SW-CF rotations, 7.6×10^{-4} μg CO_2-C μg^{-1} biomass C h^{-1} for HRSW and 3.9×10^{-4} μg CO_2-C μg^{-1} biomass C h^{-1} for the SB-SW rotations. Thus there was a 12% increase in efficiency with the HRSW rotation and a 55% increase in efficiency with the SB-SW rotation over the fallow treatments. This implies that an increase in residue decomposition over time in the fallow system will eventually decrease per unit C storage of crop residues. This can also be seen by comparing the residue inputs, which are similar (Table 2), and the total C values, which are increased, under NT continuous cropping (Table 1).

Over 5 years the effects of frequency of residue inputs, C storage and metabolic efficiency of NT continuous spring cereals over fallow systems has increased soil C by approximately 10% mostly in the POM fraction. While these are promising results, it is important to note the transient nature of the increased C pool. Compared to total C, POM C is more sensitive to management. Therefore, any changes in management or in the environment (i.e. increased temperatures) could result in large emissions of CO_2 from the soil due to the rapid decomposition of the POM.

Conclusions

Carbon storage increased under NT and continuous cropping with less C storage in the WW-F rotation due to inefficient C metabolism caused by tillage and fallow. Similarly, the lower POM content in the NT SW-CF rotation compared to the two NT continuous wheat rotations further supports the idea that fallow hinders C storage in soils even when coupled with reduced tillage. The rate of residue decomposition did not appear to be related to C storage; however, priming caused by residue additions is a loss of labile C from the soil that needs to be considered when assessing C storage in an agricultural soil. Priming is affected by and correlated with two factors: the size of the biomass, which is affected by both tillage and rotation, and perhaps more importantly the composition of the soil microflora with respect to the F:B ratio. In the early phase of decomposition priming is controlled by bacterial growth and endogenous metabolism. In later stages, it is controlled by the interaction between fungi and bacteria the extent of which is determined by the F:B ratio. It would also appear that substrate additions more than disturbance is important in the priming of microbial biomass C, which may affect long term C storage in high frequency input systems. Thus we conclude that to evaluate C storage in alternative systems multiple factors have to be interpreted. Because microbial biomass plays a role in C cycling and partitioning and is a dynamic soil constituent, a single linear hypothesis rarely seems to explain complex interactions in soil ecosystems.

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